A TAXONOMIC STUDY OF THE COOTER TURTLES, *PSEUDEMYS FLORIDANA* (LECONTE) AND *PSEUDEMYS CONCINNA* (LECONTE), IN THE LOWER RED RIVER, ATCHAFALAYA RIVER, AND MISSISSIPPI RIVER BASINS

KENNETH MARK FAHEY*
Department of Biology, The University of Southwestern Louisiana
Lafayette, Louisiana 70504

ABSTRACT

The taxonomy of the cooter turtles, *Pseudemys floridana* (LeConte) and *Pseudemys concinna* (LeConte) was studied in southwestern Louisiana to determine the relationship between these two turtles and to examine the validity of the taxonomic characters currently utilized.

One hundred and sixty-two turtles were examined from the lower Red River, the Atchafalaya River, and the Mississippi River basins. The color patterns and osteological characteristics were numerically scored. A discriminant analysis based on the characters of plastral pattern, carapace pattern, bridge markings, and the number of phalanges in the fifth toes of the hind feet, was conducted on these specimens. Two *a priori* groups of specimens with relatively "pure" characters were selected, one with *P. floridana* characters and one with *P. concinna* characters. From these *a priori* groups a set of discriminant coefficients was calculated for each character and all specimens were assigned Z-values based on these characters.

A linear plot of the Z-values showed most specimens in the sample were intermediate, with Z-values distributed between and overlapping both *a priori* groups. The four characters used had little or no taxonomic value in separating these turtles. The wide range of Z-values found within individual clutches indicated interbreeding of specimens with widely varying characteristics. Correlation coefficients for toe phalanx number and plastral pattern versus carapace length indicated these characters to be ontogenetic.

The results show that *Pseudemys floridana* and *Pseudemys concinna* should be synonymized under the senior synonym, *Pseudemys floridana*, pending discernment of quantitative characters that will distinguish *floridana* and *concinna* as species.

INTRODUCTION

The North American emydid turtles of the genus *Pseudemys* have had a long, confused taxonomic history. Relationships among many of the species complexes are neither understood nor agreed upon. *Pseudemys floridana* (LeConte) and *Pseudemys concinna* (LeConte) are members of one such complex. A taxonomic study of these two species was conducted in the lower Red River, the Atchafalaya River, and the Mississippi River basins in Louisiana (Fig. 1). The three subspecies reported to occur in this area according to Ernst and Barbour (1972), and Conant (1975) are *Pseudemys floridana hoyi* (Agassiz), *Pseudemys concinna hieroglyphica* (Holbrook), and *Pseudemys concinna mobilensis* (Holbrook). The purpose of this study was to determine the relationship between *Pseudemys floridana* and *Pseudemys concinna* in

**Present address: Department of Zoology-Entomology, Auburn University, Auburn, Alabama, 36830.*

EDITORIAL COMMITTEE FOR THIS PAPER:
DR. JOHN W. CRENSHAW, JR., Director, School of Biology, Georgia Institute of Technology, Atlanta, Georgia 30332
DR. FRANCIS L. ROSE, Professor of Biology, Texas University, Lubbock, Texas 79409

southern Louisiana and to examine the validity of the taxonomic characters currently being utilized to separate them.

Pseudemys concinna ranges throughout much of the southeastern United States and contains the subspecies *concinna, suwanniensis, mobilensis, texana* and *hieroglyphica. P. floridana* occurs in approximately the same geographic range and contains the subspecies *floridana, peninsularis*, and *hoyi* (Crenshaw, 1955; Ernst and Barbour, 1972; Conant, 1975). According to Ernst and Barbour (1972) *Pseudemys concinna* is an inland turtle that inhabits mainly rivers, preferring those with moderate currents, abundant aquatic vegetations, and rocky bottoms. It occurs, however, in almost any aquatic habitat such as lakes, ponds, swamps, tidal marshes, oxbows, and ditches. *P. floridana* inhabits any aquatic *habitat in the coastal plains, preferring* those with slow currents, soft bottoms, and abundant aquatic plants.

Figure 1. Study area which includes the Lower Red River, the Atchafalaya River, and the Mississippi River basins in Louisiana.

Taxonomic history. – The species were first described by LeConte (1830) as *Testudo floridana* and *Testudo concinna.* The early taxonomic literature (Bonaparte, 1831; Gray, 1831, 1855, 1863; Duméril and Bibron, 1835; Holbrook, 1836, 1838; Agassiz, 1857; Baur, 1893) involved primarily generic name changes and the addition of new subspecies.

Carr (1935) considered *Pseudemys floridana* and *P. concinna* to be northern and southern representatives of the same species. In LeConte's original description *P. floridana* had page priority so he selected it as the name of the species. Carr (1937) synonymized *P. mobilensis* with *P. floridana* and named a new subspecies *P.f. suwanniensis.* Stejneger (1938) recognized a new subspecies, *P.c. hoyi*, for the specimens which Agassiz had called *Ptychemys hoyi.*

Carr (1938) described *P.f. peninsularis* from Florida and included an analysis and key to the *P. floridana* group. He stated, "Due to inherent genetic instability, or to re-establishment of intercourse between previously isolated stocks, individual variation within a local population (even in a single litter) may result in phenotypes superficially more dissimilar than the actual races." He thought many descriptions stressed characters that were highly variable or sexually dimorphic and that because of this the original descriptions were inadequate. He described the *P. floridana* group as " . . . a *Rassenkreis* which extends westward in two limbs from the Atlantic coastal *floridana* – an inland series (*concinna, hieroglyphica, texana*), and another in the coastal plain (*peninsularis, suwanniensis, mobilensis*)." Carr (1952) redescribed the group and added *P.f. hoyi.*

Crenshaw (1955), in his study of the Florida races *P.f. floridana, P.f. peninsularis,* and *P.f. suwanniensis*, stated that the relationships between all turtles of this complex were best shown by subdividing the complex into two species, *P. concinna* and *P. floridana*. The species *P. concinna* included the subspecies, *concinna, mobilensis, hieroglyphica, suwanniensis,* and *texana*. The species *P. floridana* included the subspecies *floridana, peninsularis,* and *hoyi*. The present status of these turtles is that suggested by Crenshaw (1955). Many authors include these turtles in the genus *Chrysemys* (McDowell, 1964; Weaver and Rose, 1967), however this has never been uniformly accepted (Holman, 1977) and data presented by Vogt and McCoy (1979) suggest that they should be placed in the genus *Pseudemys* and separated from *Chrysemys*.

Locality records and status. – Specimens of *P. floridana* are not easily distinguished from specimens of *P. concinna* on the basis of presently utilized taxonomic characters. Reported records for the three Louisiana subspecies show that many authors are unsure of the identity of specimens and unwilling to commit themselves as to the exact ranges for each subspecies. One aspect of the problem is the paucity of specimens. Another is the wide range of characters these turtles possess and the wide geographic range they occupy.

Three subspecies occur in Texas according to Brown (1950): *P.f. hoyi, P.c. texana*, and *P.c. mobilensis*. Brown referred to all as subspecies of *Pseudemys floridana*. He noted that the distribution of *P.c. texana* was unclear and that a number of specimens from Bastrop County might prove to be intergrades with *P.f. hoyi*.

Webb (1970) listed *Pseudemys f. hoyi* as occurring in eastern Oklahoma and remarked that *P.c. heiroglyphica* probably also ranged into eastern Oklahoma where the two "occasionally hybridize."

Two subspecies are reported from Arkansas, *C.c. hieroglyphica* and *C.f. hoyi* (Conant, 1975). Michael Plummer (pers. comm. November 17, 1976) has advised me that *P. concinna* appears to predominate in Arkansas populations but that most specimens appear to have intermediate characters.

The subspecies *C.c. hieroglyphica* and *C.f. hoyi* occur in the southern third of the state of Missouri where they hybridize in nature (Anderson, 1965).

Smith (1961) treated all Illinois specimens as hybrids of *P.c. concinna* x *P.f. hoyi*. His remarks included an opinion from Crenshaw which suggested that all southern Illinois turtles be regarded as hybrids because of introgression of *P. floridana* genes into the *P. concinna* populations of the lower Mississippi River Valley. Crenshaw believed this produced an intermediate form.

Two subspecies, *C.c. hieroglyphica* and *C.f. hoyi*, occur in Kentucky (Barbour, 1971). The ranges of these turtles in Kentucky appear to be sympatric and Barbour commented that the two hybridize freely with each other. Barbour (1971) and Conant (1975) showed *C.c. hieroglyphica* and *C.f. hoyi* as occurring in approximately the same ranges in Tennessee.

Three subspecies of *C. concinna* occur in Alabama; they include *C.c. concinna, C.c. hieroglyphica*, and *C.c. mobilensis* (Conant, 1975). One subspecies of *C. floridana, C.f. floridana*, occurs in Alabama (Conant, 1975; Mount, 1976). In dealing with the subspecies of *P. concinna*, Mount (1976) stated that, " . . . the geographic variation was found to be inconsistent with previous reports and assumptions" and nearly all characters used to distinguish the subspecies had wide areas of overlap. He felt the designation of subspecies was largely arbitrary. He chose to allocate all *P. concinna* in Alabama to the subspecies *P.c. concinna* and noted that hybridization between *P. concinna* and *P. floridana* occurs frequently in the southeastern portion of the state.

Existing records for these turtles in Louisiana (Viosca, 1923, 1926; Cagle and Chaney, 1950) do not give a good indication of the species and subspecies which are found in various localities. Liner (1954) listed three Tulane specimens (TU-1104, 11046, 13618) as *P. floridana*. The first is from Vermilion Parish and the last two are from Terrebonne Parish. These specimens were examined and the data included in my statistical analysis of specimens.

Keiser and Wilson (1969) reported three subspecies of these turtles, *C.c. hieroglyphica*, *C.c. mobilensis*, and *C.f. hoyi*, from Louisiana, Keiser (1976) referred to the two species as the *Chrysemys floridana-concinna* complex and used the presence of a plastral pattern and the C-shaped mark on the second costal scutes of the carapace of *C. concinna* to separate the species. He also mentioned possible skeletal characters separating them, but noted that few Atchafalaya Basin specimens fit the descriptions of the subspecies given by Carr (1952). The localities and specimens cited by Keiser (1976) are included in this study as they constitute the core of the data from which the present study grew.

MATERIALS AND METHODS

Specimens examined. – The specimens used in this study were collected primarily from the Atchafalaya River Basin from 1975 to 1977. Specimens from the Red River and Mississippi River basins were borrowed from the Tulane University collection of amphibians and reptiles (TU). Atchafalaya River Basin specimens are from the University of Southwestern Louisiana collection of amphibians and repitles (USL). A total of 162 specimens was rexamined. All specimens collected during the course of this study were catalogued into the USL collection (Appendix I).

Method of collection. – Several types of traps (Legler, 1960) were used in the collection of adult turtles. Fish, chicken, cottonseed cakes, lettuce, and watermelon were tried as bait. Although no adult *P. floridana* or *P. concinna* were caught, adults of *P. scripta*, and *C. picta* were caught in traps. Most observations of feeding suggest that *P. floridana* and *P. concinna* are primarily vegetarian as adults (Allen, 1938; Carr, 1952; Ernst and Barbour, 1972). The abundance of natural plant foods may account for my inability to trap adult specimens even when plant materials were used as bait.

I obtained adult specimens by purchasing them from fishermen or by searching for nesting females along roads. Road collecting was most successful in the early morning from 5:00 to 8:00 A.M. (C.S.T.) and in late afternoon from 3:30 P.M. until dusk. Five adults from which I later obtained egg clutches were collected in this manner. A gill net was occasionally used in the collection of adult turtles, though with limited success.

Two methods used without success for the collection of juvenile turtles were night collecting and snorkeling. The most successful method of obtaining small turtles was to dip-net basking animals from a canoe or powerboat. Collection methods used in other areas with clear water (Chaney and Smith, 1950) did not work well in central Louisiana. The waters frequented by these turtles in central Louisiana usually are over 1 m deep and are often very turbid.

All eggs were collected from gravid females using Cagle's (1944) method. Specimens were pithed and the entire oviducts were removed. The eggs were removed from the oviducts and placed in an incubator. Five clutches were incubated using Trotter's (1973) technique, with hatching success varying from 5% to 88%. Each clutch of hatchlings was kept alive for several months for observation and to allow color patterns to become distinct.

Osteological preparations. – Phalanges of the fifth toes of the hind feet were examined by X-ray (adult specimens) or clearing and staining (hatchlings and juveniles). The clearing and staining procedure was, with modifications, that of Hardaway and Williams (1975).

Description of taxonomic characters. – A number of taxonomic characters are presently used to differentiate subspecies of *P. floridana* and *P. concinna* in various parts of their ranges. They do not apply to all the subspecies and the reliability of each character varies depending on the subspecies and the locality. As many characters as possible were examined to determine which could possibly be used to separate *P. floridana* and *P. concinna* in the area studied.

Two characters used in this study and referred to in most present taxonomic literature (Carr, 1952; Crenshaw, 1955; Ernst and Barbour, 1972; Conant, 1975) are the plastral pattern and the carapace markings. *P. concinna* is reported to have a C-shaped yellow line on the second costal scute of the carapace (Fig. 2) and a plastral pattern that generally follows the seams of the plastral scutes (Fig. 3). *P. floridana* has either a straight line or an inverted Y-shaped line on the second costal scute of the carapace (Fig. 2) and an immaculate plastron (Fig. 3). Both of these characters are presently used as the major taxonomic characters separating these species. Both are based on pigmentation which, if used alone, is not a reliable taxonomic character at the species level. Variation in color and in the arrangement of pattern can result from non-genetic factors. Temperature may play an important role in pattern determinations especially during embryonic development (Fowler, 1970; Vinegar, 1973, 1974).

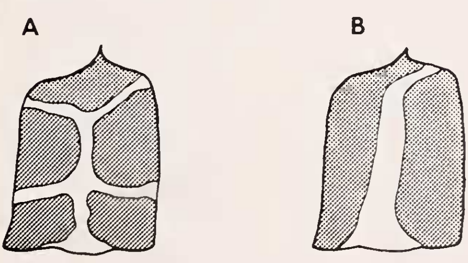

Figure 2. Pattern on the second costal scutes of the carapace; A. C-shaped pattern of *Pseudemys concinna*; B. Straight line pattern of *P. floridana*.

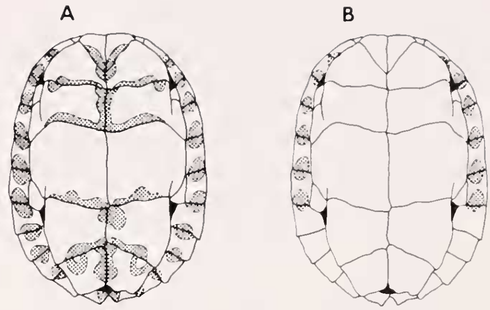

Figure 3. Typical plastral patterns; A. *Pseudemys concinna;* B. *P. floridana.*

Three characters that are used to distinguish various subspecies of *P. floridana* and *P. concinna* are neck stripe pattern, jaw serration, and the pattern on the ventral surface of the marginal scutes. All specimens in my sample were scored for each of these characters. These characters are, however, probably too qualitative and their range of variation too great to be useful in statistical analyses.

The pattern of stripes on the dorsal surface of the neck is used to distinguish *P.f. peninsularis* from *P.c. suwanniensis* in Florida. *P.f. peninsularis* has a hairpin pattern while *P.c. suwanniensis* has a series of straight lines (Fig. 4). Sample specimens were scored as continuously lined (C), discontinuously lined (D), or hairpin patterned (H), for right and left sides of the neck. Many specimens possessed different combinations of these three categories and some possessed intermediate pattern types.

Jaw serration is used to distinguish *P.c. texana* from the other subspecies of *P. concinna* and *P. floridana*. This character can also be used to distinguish three Florida turtles, *P.f. peninsularis, P.c. suwanniensis,* and *P. nelsoni*, from each other. The sample specimens were scored on the basis of whether their jaws were serrated (S) or unserrated (U) and whether the upper jaw was notched (N) or un-notched (no symbol). The range of variation included that which was found in the above mentioned species long with other variations (Fig. 5).

The pattern on the ventral surface of the marginal scutes is used to distinguish *P. concinna* subspecies from *P. floridana* subspecies in Florida. *P. floridana* reportedly has few or no marginal markings while *P. concinna* may possess a variety of

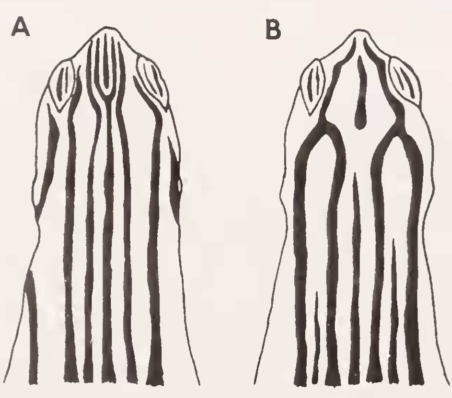

Figure 4. Neck stripe patterns; A. *Pseudemys concinna suwanniensis*; B. *P. floridana peninsularis.*

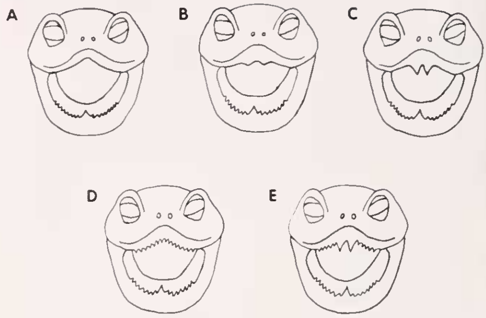

Figure 5. Jaw serrations found in various species and subspecies of *Pseudemys*; A. *P. concinna concinna*; B. *P. floridana hoyi*; C. *P. concinna texana*; D. a Louisiana variation; E. *P. nelsoni* (also found in some Louisiana specimens).

patterns (Fig. 6). Three predominant patterns occurred in the sample, but a fourth type, the absence of markings, was not observed. Patterns were scored as types one to four (Fig. 6).

A character I have analyzed in detail is the number of phalanges of the fifth toes of the hind feet (Weaver and Rose, 1967). Associated with this is the fusion or separation of the astragalus and calcaneum in the ankle (pers. comm. June 17, 1976, with unpublished manuscript attached from Francis L. Rose). These characters, when first used by Weaver and Rose (1967) in their study of the genus *Chrysemys*, appeared to be different for *P. floridana* and *P. concinna*. *P. floridana* reportedly had two toe phalanges and a fused astragalus and calcaneum. *P. concinna* reportedly had three toe phalanges and a separated astragulus and calcaneum (Fig. 7). These differences were theorized to be related to the degree of terrestrial or aquatic habits of each species (unpublished manuscript from Francis L. Rose). *P. floridana*, the more terrestrial turtle, has a shorter fifth toe and a more solid foot for better support while walking on land. *P. concinna* has a longer fifth toe which allows increased webbing; the separate astragalus and calcaneum al-

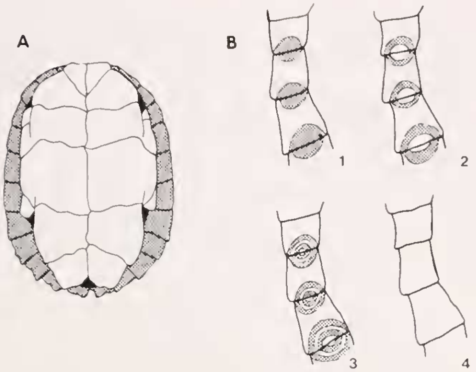

Figure 6. A. Locations of the pattern on the ventral surfaces of the marginal scutes. B. Pattern types found on the ventral surfaces of the marginals and the numerical scoring used to classify these.

so make its foot more flexible for swimming. Rose (pers. comm. October 11, 1976) has states that these characters may or may not be good taxonomic characters.

Penial morphology of *P. floridana* and *P. concinna* was shown to be identical with that of *P. scripta* and *P. nelsoni* (Zug, 1966). Osteological characteristics of the skulls of emydid turtles were analyzed and used for taxonomic purposes by McDowell (1964). He drew a distinction between a *rubriventris* series and a *floridana* series but did not identify any differences between *P. floridana* and *P. concinna*. Skull osteology and penial morphology were not examined in this study.

The precopulatory behavior reported for *P. floridana* (Cagle, 1950) appears to be similar to that reported for *P. concinna* (Marchand, 1944; C.G. Jackson, 1972). If there are subtle behavioral differences between *P. concinna* and *P. floridana* they have not been reported.

Statistical methods. – Markings from the following body and shell regions were recorded for each specimen: carapace, plastron, neck, bridge, and marginal scutes. Toe phalanx number on the fifth toes of the hind feet, fusion of the astragalus to calcaneum, jaw serration, and carapace length were also recorded. The color pattern data were qualitative and various systems of scoring patterns were devised for quantifying these data. The scoring systems used in this study were based on the key characters that have been used to separate *P. floridana* and *P. concinna* as species.

Plastral pattern was quantified by counting the number of plastral scutes that contained dark pigmentation. A number ranging from 0 to 12 was assigned to each turtle on the basis of the number of scutes containing dark pigmentation (Fig. 8). Most literature describes *P. floridana* as having an immaculate plastron, however, very few specimens in my sample completely lacked dark plastral pigmentation. I assumed individuals with low scores to be of *P. floridana* stock.

Pattern on the second costal scutes of the carapace was more difficult to score. When a large sample of specimens was examined, a gradation from the straight-line pattern of *P. floridana* to the C-shape of *P. concinna* could be observed. Five numbered categories were defined and numerical scores were assigned as follows: straight-line (1), branching (2), Y-shaped (3), X-shaped (4), and C-shaped

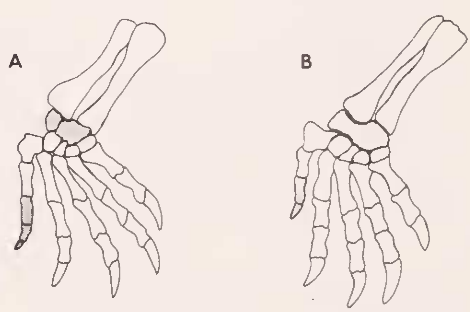

Figure 7. Bones of the hind feet; A. *Pseudemys concinna*, showing three phalanges on the fifth toe and separate astragalus and calcaneum; B. *P. floridana*, showing two phalanges on the fifth toe and a fused astragalus and calcaneum.

(5) (Fig. 9). The decision between an X-shaped and a C-shaped pattern was based upon whether the posterior branches touched the neural and marginal scutes (Fig. 9-4; X-shaped) or touched the third costal scute (Fig. 9-5; C-shaped). In some cases, especially in older specimens, this was difficult to accurately determine. If the branches were not complete a judgment as to their general direction had to be made. Right and left costal patterns were scored separately and later summed.

Four scutes make up the bridge that connects the plastron to the carapace. Specimens were scored 0 through 4 for left and right bridges separately, according to the number of scutes with dark pigmentation (Fig. 10). Scores for right and left sides were later summed. Neck striping and marginal markings were too qualitative and variable to be used in the statistical analyses.

Toe phalanx numbers on the fifth toes of the hind feet were recorded separately and later summed for use in the discriminant analysis. The astragalus fused to the calcaneum was not used since these bones were separate in all but three specimens.

A discriminant function based on four characters (plastral pattern, carapace pattern, bridge markings, and toe phalanx number) was computed using the

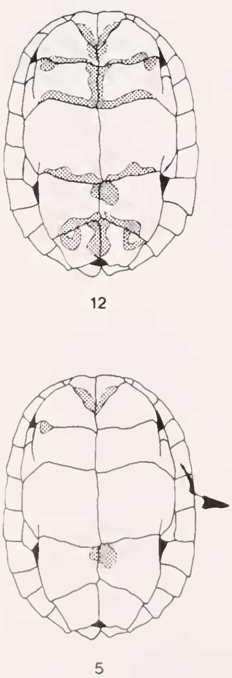

Figure 8. The scoring system for plastral patterns. Numbers indicate the number of plastral scutes containing dark pigmentation.

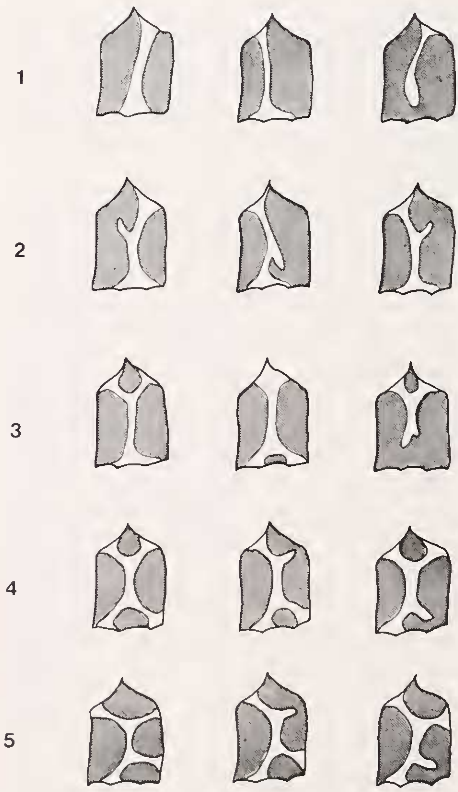

Figure 9. Scoring system used for the second costal scutes of the carapace; (1) Straight-line; (2) Branching; (3) Y-shaped; (4) X-shaped; (5) C-shaped. Three variations are shown for each category.

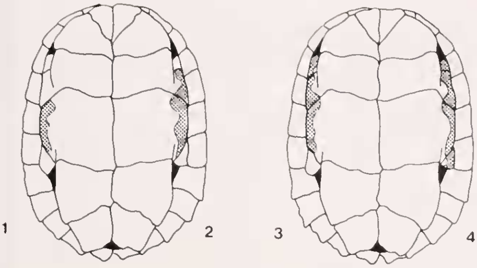

Figure 10. Scoring system used for scutes making up the bridge. Pattern categories 1 through 4 are shown through a 0 category could also be found.

BMD-04M program (Dixon, 1973). This program develops the linear function of the selected variables that gives the largest ratio of between-group variance to within-group variance. A series of discriminant coefficients is calculated to give this ratio and thus maximize discrimination between two *a priori* groups (Rao, 1952; Krishnaiah, 1966; Kendall, 1968; Gnanadesikan, 1977).

In accordance with this program, two *a priori* groups of twenty individuals each were selected from the total sample of 162 specimens; one group of specimens exhibited "pure" *P. floridana* characters, and the other "pure" *P. concinna* characters. Age and sex were not a basis for the selection of the *a priori* groups. From these *a priori* groups the set of discriminant coefficients was calculated. The sum of these coefficients times their respective character scores gave a value Z for each specimen. Using these Z-values, the program automatically classified into one group or the other all specimens not included in the *a priori* groups. By writing an addition to the program the Z-values themselves were obtained. Plotting individual Z-values on the discriminant axis showed which specimens in the unknown sample were within the range of either *a priori* group and which were intermediate (Rohwer and Kilgore, 1968; Thaeler, 1968; J.F. Jackson, 1973).

In addition to the discriminant analysis, correlation coefficients among several characters were computed using the BMD-02D program (Dixon, 1973). This program computes simple correlation coefficients. Early in this study I noticed that plastral pattern appeared to fade with age and that the number of toe phalanges on the fifth toes of the hind feet seemed to increase from 2 to 3 with age. Correlation coefficients between these characters and carapace length were computed to determine if this relationship actually existed.

RESULTS

Statistical analyses. – The results of the discriminant analysis (Fig. 11A) clearly show that, based on Z-values calculated from the four characters used, the sample does not fall into two distinct groups (species). There is also no large intermediate group that would indicate only F_1 hybridization. The sample is instead evenly distributed between, and overlaps, each *a priori* group. This indicates interbreeding of *P. concinna* and *P. floridana*, and backcrossing and interbreeding of the hybrids.

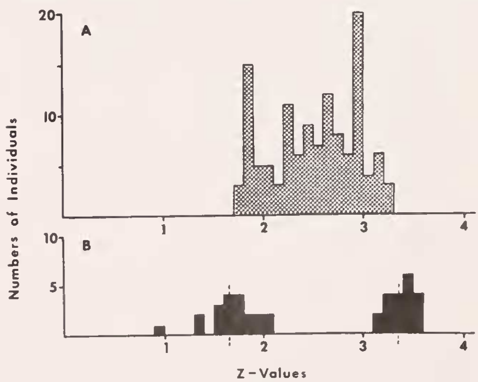

Figure 11. Histograms of specimen Z-values on discriminant axes; A. Plot of the Z-values of the unknown sample in the discriminant analysis; B. Plot of the Z-values of the *a priori* groups of *Pseudemys concinna* (mean 3.36) and *P. floridana* (mean 1.66). Dashed lines indicate the means of the *a priori* groups.

Table 1. Results of the discriminant analysis. Mean scores for each of the four characters used are shown for each *a priori* group along with the discriminant coefficient for each of the characters. Sample size, mean Z-value, and standard deviation for these Z-values are also given. Left and right scores have been summed for each character.

Character	*P. floridana* mean	*P. concinna* mean	Discriminant coefficient
1. Carapace pattern	3.150	9.650	0.149
2. Plastral pattern	4.850	9.750	0.037
3. Toe phalanx number	3.900	6.000	0.251
4. Bridge markings	5.350	7.750	0.007

a priori group	Sample size	Mean Z	Standard deviation Z
P. floridana	20	1.663	0.273
P. concinna	20	3.359	0.120

The mean Z-value of the *P. floridana* (1.66) and the *P. concinna* (3.36) *a priori* groups (Table 1) are well separated and the ranges of these groups have no overlap (Fig. 11B). The means for each character are also well separated (Table 1).

The range of the *P. floridana "a priori"* group was 1.14 (0.91 to 2.05) and that of the *P. concinna "a priori"* group was 0.38 (3.12 to 3.50). The range of the intermediate zone was 1.07 (2.05 to 3.12). This was slightly smaller than the range of the *P. floridana "a priori"* group. The unknown sample fills the intermediate zone, and overlaps and completely connects both *a priori* groups. Of the unknown individuals measured, 27 had Z-values that overlapped the *P. floridana "a priori"* group and 11 had Z-values that overlapped the *P. concinna "a priori"* group.

The Z-values for individuals from the five clutches hatched during this study were plotted, along with the Z-values of the females from which they were obtained, on separate discriminant axes (Fig. 12). In these figures the linear placement of genetically related individuals in the discriminant analysis is seen. In each plot the outlines of the *a priori* groups are shown. Specimens from the clutches used to make up part of the *a priori* groups are indicated by stippled squares.

Correlations computed on plastral pattern and toe phalanx number versus carapace length indicate these characters to be ontogenetically variable and not useable in taxonomy. The correlation of plastral pattern to carapace length was -0.40 which suggests a disappearance in the amount of plastral pattern as turtles grow. The correlation of toe phalanx number to carapace length was 0.45, which suggests that as turtles grow, a third phalanx on the fifth toes of the hind feet ossifies.

Qualitative characters. – Scoring of the characters jaw serration (Fig. 5), neck striping (Fig. 4), and marginal scute pattern (Fig. 6) is shown in Table 2. Jaw serration followed a gradient from strongly serrated to slighty serrated.

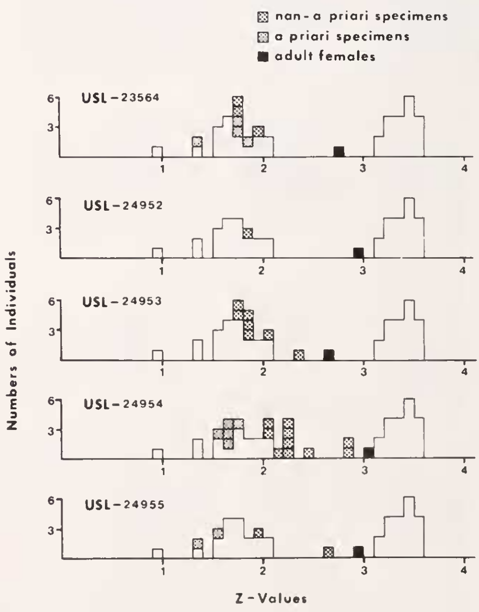

Figure 12. Plots on separate discriminant axes of the Z-values for the individual clutches from USL 23564, USL 24952, USL 24953, USL 24954, and USL 24955. Outlines of the *a priori* groups are shown. Individual specimens that were used to make up part of an *a priori* are shown by stippled squares and those not originally included in the *a priori* groups are shown by cross-hatched squares. The female from which each clutch came are shown as black squares.

For marginal scute patterns most specimens were scored as either type 2 (25.0%), with a doughnut-shaped mark, or type 3 (59.3%), with a double dougnut-shaped mark (Table 2; Fig. 6). Specimens were classified on the basis of the predominant pattern. Many specimens possessed several different types of markings.

Specimens scored for neck stripes (Fig. 4) possessed either continuous lines (31.4%) or hairpins (38.9%) on both sides of the neck. Fewer had discontinuous lines (12.5%) on both sides and the rest of the sample had mixed patterns (Table 2).

Analysis of clutches. – Data from 34 hatchlings, obtained from the five gravid females, were included in the statistical analyses. Thirty-five eggs hatched, with an average incubation time of 60 days at 29° C. Many hatchlings had irregularities of shell scutes possibly caused by excessive incubation temperatures (Fowler, 1970; Vinegar, 1973, 1974). Details of each clutch are presented below:

USL 23564. – Eight individuals were hatched from the nine eggs of this female. The adult female predominantly resembled a *P. floridana*, however, the discriminant analysis placed this specimen as intermediate (Z-value of 2.70) and widely separated from its hatchlings. Seven of the hatchlings were used in discriminant analysis. One hatchling was lost. Four of the hatchlings were used to make up part of the *P. floridana "a priori"* group and the other three had Z-values that were clustered around the means of the *P. floridana "a priori"* group. Hatchlings Z-values ranged from 1.33 to 1.99 (Fig. 12). The hatchlings are catalogued as USL 24113–24119.

USL 24952. – Only one individual was hatched from 14 eggs taken from this female from Avoca Island, St. Mary Parish. The Z-value of the adult was 2.90 and

Tabla 2. Results of scoring the qualitative characters. Numbers of specimens for each category and percentages of the total sample are given for each character. Jaw serration and marginal scute pattern acoring systems are given in Figs. 5 and 6 respectively. Neck stripes were scored for left and right sides as: C - continuous lines, D - discontinuous lines, and H - Hairpin pattern.

Jaw serrations			
Serrated		Unserrated	
Notched (SN)	Un-notched (S)	Notched (UN)	Un-notched
54 / 33.5%	35 / 21.7 %	10 / 6.2 %	62 / 38.5 %

Marginal Scute Pattern			
Type 1	Type 2	Type 3	Type 4
25 / 15.6%	95 / 59.3%	40 / 25.0%	0 / 0.0%

Neck Stripe Pattern					
C-C	H-H	D-D	C-H	C-D	H-D
50 / 31.4%	62 / 38.9%	20 / 12.5%	15 / 9.4%	3 / 1.8%	9 / 5.6%

close to the *P. concinna "a priori"* group's range though it superficially resembled a *P. floridana*. The hatchling had a Z-value of 1.87 which was within the range of the *P. floridana* "a priori" group (Fig. 12). The hatchling is catalogued as USL 24986.

USL 24953. – Seven individuals with scorable patterns hatched from 15 eggs of this female. The adult, also collected at Avoca Island, superficially resembled a *P. floridana*. All hatchlings possessed heavily pigmented plastra. The Z-values of the hatchlings ranged from 1.79 to 2.30 with all but one within the range of the *P. floridana "a priori"* group. The adult's Z-value was 2.60 which was well separated from all but that of one hatchling (Fig. 12). The hatchlings are catalogued as USL 24987 to 24993.

USL 24954. – The largest clutch came from this Avoca Island female. The adult possessed some *floridana*-like and some *concinna*-like characters. Fifteen hatchlings were obtained from 16 eggs. The hatchlings had a wide variety and combination of characters. The Z-values of these hatchlings ranged from 1.54 to 2.89. Five specimens from this clutch were used to make up part of the *P. floridana "a priori"* group. The majority of the hatchlings, however, had Z-values that placed them between the ranges of the two *a priori* groups. The female had a Z-value (3.01) which was greater than all the hatchlings' and was well separated from all but two of the hatchlings (Fig. 12). The hatchlings are catalogued as USL 24967 – 24982.

USL 24955. – Seven eggs were taken from this female. From these, one hatchling was obtained and three embryos were removed from eggs in an advanced enough stage of development for their patterns to be scored. The adult was collected from the Atchafalaya River at Butte La Rose, St. Martin Parish. The Z-values for this clutch had the widest range of all the clutches analyzed (1.30 to 2.66). Here, as in the other clutches, the adult female had a Z-value (2.90) that was well separated from those of the hatchlings. Two of the hatchlings were used to make up part of the *P. floridana* "*a priori*" group (Fig. 12). The hatchlings are catalogued as USL 24982 – 24985.

DISCUSSION

The results from the discriminant analysis (Figs. 11 and 12; Table 1) show that the majority of the sample is intermediate on the basis of the four characters considered (plastral pattern, carapace pattern, bridge markings, and toe phalanx number). Other characters were not used in this analysis because of their wide and inconsistent range of variability. If the Z-values derived from these four characters can be assumed to be a measure of the genome then there is a complete gradation of characters from *floridana*-like to *concinna*-like individuals.

The *a priori* groups were selected by looking through the entire sample of 162 specimens and picking those whose characters nearly all were *floridana*-like or *concinna*-like. Age and sex were not used as criteria for the selection of the *a priori* groups. Calculations of Z-values show that some individuals from the unknown sample would evidently have been better choices for the *a priori* groups than some of the specimens selected. Using a sample size of 20 for each *a priori* group necessitated inclusion of some individuals whose characters were not all one extreme or the other.

If *P. floridana* and *P. concinna* were distinct species several results would be expected from the discriminant analysis. There would be a clustering of the unknown individuals around the *a priori* group means. There could be an F_1 hybrid peak somewhere between the two *a priori* groups but there should not be an even and continuous distribution of specimens from one *a priori* group to the other. The results are inconsistent with this and do not support the idea of separate species.

Figure 12 shows that all the clutches examined have a fairly wide range of characters. The clutches from USL 23564 and 24593 are grouped around the *P. floridana* "*a priori*" group. In the clutches from USL 24952, 24954, and 24955 the hatchlings' and adults' Z-values are widespread. The clutch from USL 24954 in particular has a wide range of Z-values that extend from one *a priori* group to the other. In each clutch the adult turtle's Z-value was separated from those of the majority of the hatchlings. The wide spread Z-values of these clutches and the separation of the majority of the hatchlings' Z-values from those of the adult females' are good indications of intergradation.

If *P. floridana* and *P. concinna* could be separated by a set of characters then the characters used to define each species should have a high degree of correlation. During the collection of data for this analysis I noticed that plastral pattern and toe phalanx number seemed to be related to the size of the individuals. The correlation coefficients for these characters to carapace length also indicate this. Both toe phalanx number (correlation coefficient of -0.45) and plastral pattern (correlation coefficient of + 0.40) have a high correlation to shell length; this suggests that these characters are ontogenetic and of limited use as taxonomic characters. These characters were nevertheless used in the discriminant analysis since there were observable differences in them within the sample and no other characters were available.

The problem is whether these turtles should be regarded as separate species that are hybridizing or as subspecies that are intergrading. Perhaps as Carr (1952) stated, they do not fit well into our standard classification system. This problem has been compounded by several factors. Many of the original descriptions of these turtles are of limited use because the separation of species was based on locality and on sexually dimorphic characters. Their taxonomy at the present is based only on qualitative characters of color and pattern. Most studies of these species have dealt with only small segments of the ranges of these turtles.

In the original descriptions Le Conte (1830) described *Testudo floridana* and *T. concinna* and differentiated between them primarily on the basis of color and pattern. He mentioned differences in the shape of the carapacial scutes which can probably be attributed to the sex and size of the specimens used in his descriptions. The *T. floridana* he described was 15 inches (37.5 cm) long and the *T. concinna* was only 8 inches (20.3 cm) long. Carapacial scutes change shape as the turtles grow. Other than these scute differences LeConte differentiated between the two only by the pattern of yellow lines on the carapace.

Holbrook (1836 to 1838) described *Fmys hieroglyphica* and *E. mobilensis,* and also listed *E. concinna* and *E. floridana.* His descriptions, like those of LeConte, were based primarily on color and pattern. He also relied heavily on the location from which the specimens were taken for identification. His descriptions of all four turtles were similar; major differences were related mostly to sexually dimorphic and ontogenetic characters of the specimens.

All populations studied by Carr (1935, 1937, 1938, 1952) were considered by him to be subspecies of *P. floridana* since wherever any came into contact they interbred, and no characters could be used to reliably separate them. There appeared to be one exception to his uniform intergradation. Two of the subspecies, *P.f. peninsularis* and *P.f. suwanniensis*, seemed to maintain nearly complete reproductive isolation. The other subspecies *of P. floridana* were geographic subspecies; *P.f. peninsularis* and *P.f. suwanniensis* appeared to be ecological subspecies, separated by the preference of different habitats.

Crenshaw's (1955) division of the *P. floridana* complex into two species is based on the reproductive isolation maintained between *P.c. suwanniensis* and *P.f. peninsularis*. This division is founded upon an exception and not what normally occurs throughout the species ranges.

Crenshaw mentioned the occasional hybridization between *P.f. peninsularis* and *P.c. suwanniensis* but stated that it was believed to be secondary intergradation and rare. He also stated, "Evidence of introgressive hybridization and frequency of strongly intermediate specimens of the *floridana* and *concinna* groups increases progressively as one moves away from peninsular Florida into other areas of the U.S., however, relatively typical examples of each group occur throughout the area of geographic overlap of the two groups."

Crenshaw concluded that, "Relationships between members of the *P. floridana* complex will be more nearly reflected by subdividing the complex into two species." This was true for *P.f. peninsularis* and *P.c. suwanniensis* in Florida but not for the other subspecies throughout their respective ranges. Along with work of other researchers, my data indicate a large amount of intergradation in most areas of the ranges of these turtles (Smith, 1961; Pritchard, 1967; Barbour, 1971; Keiser, 1976; Mount, 1976). Crenshaw's work showed that *P. concinna* and *P. floridana* were closely related and intergrading but it did not conclusively show that they should be regarded as separate species.

Pritchard (1967) is the only recent author who has followed Carr's scheme. He mentioned difficulty in identification of subspecies because of extensive hybridization and the fact that some of the subspecies are not easily distinguishable from one another. He felt that separation into *P. floridana* and *P. concinna* was incorrect since the two intergrade completely.

Mayr (1963) defined species as, "groups of interbreeding natural populations that are reproductively isolated from other such groups." This definition is based primarily on reproductive isolation. Mayr listed various situations in which it would be difficult to apply this definition. Four of these situations are (1) morphological differentiation without reproductive isolation, (2) reproductive isolation dependent upon habitat isolation, (3) incompleteness of isolating mechanisms, and (4) the achievement of different levels of speciation within different populations. These four situations have possible application to the *P. floridana–concinna* complex.

Some authors (Ernst and Barbour, 1972; Conant, 1975) indicate that *P. floridana* and *P. concinna* occupy or once occupied different habitats. Possibly they have differentiated morphologically because of the different selective pressures in these habitats but have not developed any form of reproductive isolation before re-establishing contact with each other. Without reproductive isolation turtles differing morphologically may have interbred, producing offspring with a variety of characteristics. Many of these characteristics may not be useable as taxonomic characters to separate the two as species.

My data indicate that in the lower Red, Atchafalaya, and Mississippi river basins there is a large amount of interbreeding. Other workers (Brown, 1950; Smith, 1961; Anderson, 1965; Webb, 1970; Barbour, 1971; Mount, 1976) have also indicated the occurrence of interbreeding in other areas. The isolating mechanisms, if they exist, do not appear to be well established. Even in Florida the reproductive isolation of *P.f. peninsularis* and *P.c. suwanniensis* is not complete though interbreeding is rare (Crenshaw, 1952).

In nearly all areas of contact between *P. floridana* and *P. concinna* interbreeding has been observed, but in a few areas where there are distinct and separate habitats, interbreeding is rare (Smith, 1961; Pritchard, 1967; Barbour, 1971; Keiser, 1976; Mount, 1976). Contact between populations seems to be the most important limiting factor of reproductive isolation.

The lower Mississippi River drainage in Louisiana is an area where frequent contact between these turtles could be expected. Here the aquatic habitats are not as well defined as in many other areas of these species' ranges. Periodic flooding tends to mix geographically separated populations more often. Because of the increased contact *P. floridana* and *P. concinna* probably interbreed more in this area than in many others and as a result have greater genetic similarity here.

Though Mayr (1963) stresses reproductive isolation as the prime factor separating species, it is not synonymous with noninterbreeding. Two species can interbreed and be reproductively isolated (Bigelow, 1965). Interbreeding can occur with little effect if the progeny are incompatible with the parent species. What is important is the flow or introgression of genes from one species to the other. My data indicate that introgression has taken place and implies a high degree of compatibility between *P. floridana* and *P. concinna*.

Grant (1963) described various population systems and used the term "semispecies" to refer to a population system having properties of both races and species. Following his classification system *P. floridana* and *P. concinna* would be classified as "sympatric semispecies" which are, "population systems intergrading discontinuously or partially and judged to be interbreeding on a restricted scale, they are sympatric and only partially isolated reproductively." Grant's classification offers a basis for argument that *P. floridana* and *P. concinna* are "ecological races" which are, "population systems intergrading continuously in morphological or physiological characters and judged to be interbreeding freely." Grant's classification would not classify *P. floridana* and *P. concinna* as separate species.

Both Grant's and Mayr's systems for classifying populations and species are useful as possible explanations of the relationship between *P. floridana* and *P. concinna*. The exact nature of the relationship cannot be determined except by long term breeding experiments. There is definite intergradation within the lower Red, Atchafalaya, and Mississippi river basins. The isolating mechanisms between *P. floridana* and *P. concinna* are weak if they exist. There is a complete gradation of characters and the characters presently used to separate these turtles into two species are probably useless. Apparently either a large hybrid swarm (a population that forms a continuous bridge between two parental species due to a breakdown in the isolating mechanisms) is present or two or more subspecies are merging within this area.

CONCLUSIONS

1. The discriminant analysis based on four characters (plastral pattern, carapace pattern, toe phalanx number, and bridge markings) has shown the following:
   - A. The specimens of the sample were not distinguishable as *Pseudemys floridana* and *P. concinna* but the majority were instead intermediate.
   - B. These four characters are of little or no taxonomic value in separating these turtles since there was found to be a complete and even gradation from *floridana*-like to *concinna*-like specimens.
   - C. The wide range of Z-values found within individual clutches indicates interbreeding of specimens with widely varying characteristics.

2. Plastral pattern was found to fade with age and was highly variable within individual clutches. This character is of little or no taxonomic value for the separation of *P. concinna* and *P. floridana*.

3. Toe phalanx number on the fifth toes of the hind feet appears to increase from two to three with age and is of little or no taxonomic value for the separation of *P. concinna* and *P. floridana*.

4. Because the majority of the sample of Louisiana specimens possesses inter-

mediate characters, and appears to be part of one continuously interbreeding population, I propose that the scheme of Carr (1952) be followed. Accordingly *Pseudemys concinna* and *Pseudemys floridana* are synonymized under the senior synonym, *Pseudemys floridana* until there may be quantitative characters to definitively distinguish the forms *floridana* and *concinna* as separate species.

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APPENDIX I

USL and Tulane University specimens used in the statistical analyses of this tudy. Specimens are listed by locality and parish alphabetically.

USL specimens. – Big Alabama Bayou (Point Coupee): 24034, 24094-24100, 25017. Little Alabama Bayou (Point Coupee): 23646, 23647, 24101-24106, 25018-25047, 25054-25057. East Outer Levee 5 mi. N. 1-10 (Point Coupee): 25011-25013. False River (Point Coupee): 20195. Bayou Courtableau (St. Landry): 23566-23577, 24024-24026, 24028-24029, 24033, 25048-25052. Bayou Courtableau at West Outer Levee (St. Landry): 25014-25016. Indian Bayou Hunting Club (St. Landry): 22222. Krotz Springs (St. Landry): 23261. Atchafalaya River (St. Martin): 24955, 24982-24985. Butte La Rose (St. Martin): 25053. Butte La Rose Bayou (St. Martin): 14170, 14383, 14484, 15113, 23565, 25062. Whiskey Bay (St. Martin): 23564, 24113-24119, 25058. Avoca Island (St. Mary): 24952-24954, 24967-24981, 24986-24993.

Tulane specimens. – Caddo Lake (Caddo): 458, 632, 633, 647, 657, 658, 734, 735. Tensas River, Clayton (Concordia): 16042.0-16042.6. Lake Providence (East Carroll): 826. Waggamon Pond (Jefferson): 5772-5774, 5874, 5879, 5975, 5876. Lake Arthur (Jefferson Davis): 1104. Bayou Gauche (St. Charles): 13756.2. Lake Pontchartrain (St. Charles): 13571, 16038. Chauvin (Terrebone): 13618.

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